Chapter 3
Colonization of Parasites and Vectors

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Abstract Colonization comprises the physical arrival of a species in a new area, but also its successful establishment within the local community. Oceanic islands, like the Hawaiian and the Galapagos archipelagos, represent excellent systems to study the mechanisms of colonization because of their historical isolation. In this chapter, we first review some of the major mechanisms by which parasites and vectors could arrive to an oceanic island, both naturally or due to human activities, and the factors that may influence their successful establishment in the insular host community. We then explore examples of natural and anthropogenic colonization of the Galapagos Islands by parasites and vectors, focusing on one or more case studies that best represent the diversity of colonization mechanisms that has shaped parasite distribution in the archipelago. Finally, we discuss future directions for research on parasite and vector colonization in Galapagos Islands.

Keywords Dispersal • Spread • Introduction • Coevolution • lHost specificity • Endemism

3.1 General Introduction

Colonization, in its biological sense, can be defined as the process by which species spread to new areas. It implies not only the physical arrival of the species, but also its successful establishment within the local community. Oceanic islands, like the

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Hawaiian and the Galapagos archipelagos, represent excellent systems to study the mechanisms of colonization because of their historical isolation. Ecosystem isolation was one of the most important premises used by MacArthur and Wilson (1967) for postulating the theory of Island Biogeography. In this landmark theory, they proposed that the number of species present in an isolated natural community is determined by both immigration and extinction rates. Immigration rates depend on the distance separating the island from potential sources of colonization (distance effect), while the size of the island limits resource and habitat availability and influences species extinction rates (species-area effect).

The theory of Island Biogeography has also been applied to the colonization of hosts by parasites (Poulin 2004; Reperant 2009). In this case, host mobility or density are considered distance effects influencing parasite immigration rate, and host body size and life-span represent species-area effects on extinction rate. However, the observed patterns of parasite species richness do not always fit these simple general laws of biogeography due to the complexity of host-parasite interactions and co-evolution (Poulin 2004; Strona and Fattorini 2014).

It is important to note that the term colonization usually refers to natural establishment. Humans have deeply changed the distribution of species and their environment, and human-aided spread of species to new areas is typically called invasion or introduction. Although this chapter is entitled colonization, it explores both natural and anthropogenic colonization of the Galapagos archipelago by parasites and disease vectors. Throughout this chapter, a broad definition of parasite will be used to include viruses, bacteria, protozoans, fungi, as well as more traditionally defined parasites such as arthropods or helminths.

In this chapter, we first review some of the major mechanisms by which parasites and vectors could arrive to an oceanic island, both naturally or due to human activities (see Table 3.1), and the factors that may influence their successful establishment in the insular host community. This introduction is not intended as an extensive review of species colonization, but rather as a way to place our understanding of parasite and vector colonization in Galapagos in a global context. In the following sections of the chapter, we then explore examples of natural and anthropogenic colonization of the Galapagos Islands by parasites and vectors, focusing on one or more case studies that best represent the diversity of colonization mechanisms that has shaped parasite distribution in the archipelago.

3.2 Parasite Arrival and Establishment in Islands: Overview of General Mechanisms

3.2.1 Natural Immigration

3.2.1.1 Direct Dispersal of Parasites

Some parasites may cover large distances without the help of a host or vector. Such direct immigration can be the result of active dispersal, and this mechanism is typically restricted to larger arthropod parasites or parasitoids with strong flying

Table 3.1 List of possible arrival modes of parasites and disease vectors in islands with examples and references cited in the text

Mode of arrival	Examples presented	References
Natural immigration		
Active direct dispersal	Parasitic wasp in Tasmania	Iqbal and Austin (2002)
	Parasitic wasp in Fiji	Masner and Johnson (2007)
Passive direct dispersal		
a. Aerial dispersal	Sugarcane rust, coffee leaf rust	Brown and Hovmoller (2002)
	Food and mouth disease virus	Keeling et al. (2001)
	Avian influenza virus	Ypma et al. (2013)
b. Water dispersal	*Vibrio cholera*	Hall-Stoodley and Stoodley (2005)
	Toxoplasma gondii	Conrad et al. (2005) and Lindsay and Dubey (2009)
Immigration with hosts		
a. Colonizing hosts	Plasmodium in lesser Antilles birds	Fallon et al. (2005)
	Hepatozoon sp. in New Zealand and Seychelles	Godfrey et al. (2011) and Harris et al. (2011)
b. Host switch after colonization	Helminth of Hawaii stream fishes	Font (2003)
c. Seabird breeding colonies	Seabirds of Iles Eparse	McCoy et al. (2016)
d. Migrating birds	Global spread of avian flu	Kilpatrick et al. (2006a, b), Olsen et al. (2006)
	Global spread of Lyme disease	Olsen et al. (1995)
Immigration with vector		
a. Wind dispersal of vectors	Japanese encephalitis virus	Ritchie and Rochester (2001)
	Bluetongue virus in Europe	Carpenter et al. (2009)
b. Vectors on host	Ticks on seabirds	Dietrich et al. (2011)
Anthropogenic introduction		
Infected invasive animals	Rats and trypanosoma in Christmas Island	Wyatt et al. (2008)
Infected domestic animals	Pigeon and Trichomonas in Mauritius	Bunbury et al. (2008)
	Avian plasmodium and avian pox in Hawaii	Warner (1968), van Riper et al. (1986), van Riper et al. (2002)
Game animal		Diamond and Veitch (1981)
Introduction of vector		
a. By commercial air transport	Culicid species in Pacific Islands	Lounibos (2002)
b. By commercial ship	Culicid species in Pacific Islands	Lounibos (2002)
Pathogen as a biocontrol agent	Myxoma virus in Australia	Fenner et al. (1957)

capacity such as parasitic wasps (Iqbal and Austin 2002; Masner and Johnson 2007). Other parasitic microorganisms have motile, free-living stages, but the distances they can travel are measured in centimeters rather than kilometers, and these short dispersals generally involve host-seeking behaviors. For instance, skin-penetrating nematodes such as hookworms can move quickly in the soil as they search for hosts using chemical cues (Castelletto et al. 2014), and uniflagellated zoospores of the highly lethal *Batrachochytrium dendrobatidis*—a widespread amphibian pathogenic fungus—can only swim for 24 h over few centimeters in still medium (Piotrowski et al. 2004). Thus, we do not consider host-seeking movements as active dispersal, at least not at a scale relevant to colonization of remote islands.

Parasites with limited or no active dispersal can still directly travel long distances under favorable environmental conditions. The aerial dispersal of plant pathogens, especially fungal spores, has largely contributed to the global spread of important crop diseases like the sugarcane rust or coffee leaf rust (Brown and Hovmoller 2002). Some animal pathogens can also survive several days or weeks outside of their host and can be spread by aerosols and reach naive hosts. Notably, wind dispersal has played a role in various outbreaks of foot and mouth disease virus and avian influenza virus in Europe (Keeling et al. 2001; Ypma et al. 2013). Other parasites may use water currents to reach new areas. Pathogenic bacterial species such as *Vibrio cholera* can form biofilms in marine and freshwater environments, facilitating their persistence and dispersal (Hall-Stoodley and Stoodley 2005). The protozoan *Toxoplasma gondii* can survive in seawater for up to 24 months and remain infective, and oocysts shed with felid feces in freshwater runoff are a likely source of infections in marine ecosystems (Conrad et al. 2005; Lindsay and Dubey 2009).

3.2.1.2 Immigration with Hosts

Long-distance travel of infected hosts is probably the most frequent natural mode of parasite immigration to islands. Ancestors of endemic species may have brought their parasites with them, leading to their coevolution in isolation. Such patterns can be found in some malaria parasite lineages restricted to endemic avian hosts in the Lesser Antilles (Fallon et al. 2005), or in *Hepatozoon* parasites of endemic reptiles in Seychelles or New Zealand (Godfrey et al. 2011; Harris et al. 2011). Newly arrived parasites can also switch to local hosts, sometimes even distantly related to their original host. This is the case for native helminth parasites of Hawaiian stream fishes that most likely colonized the islands with native fish-eating birds and marine fishes (Font 2003).

Many seabird species form large breeding colonies on islands for several months each year. The breeding grounds and foraging areas of multiple species can overlap, favoring parasite exchange (McCoy et al. 2016). Although seabirds often show high breeding site fidelity, colonies can be visited by transient birds (e.g., immature birds, failed breeders) or by infested birds deserting their colonies, which facilitates the colonization of new locations by parasites (Brown and Brown 2004; Dietrich et al. 2011). Many bird species also naturally travel long distances and may use islands as stop-over sites during their migration or foraging, carrying along parasites. Wild migrating birds and seabirds play an important role in the global spread of avian influenza and Lyme disease, respectively (Olsen et al. 1995; Olsen et al. 2006; Kilpatrick et al. 2006a).

3.2.1.3 Immigration with Arthropod Vector

Some disease vectors such as mosquitoes or midges are also capable of traveling long distances, usually with the help of aerial currents, and may bring parasites with them to new areas. For example, wind dispersal of infected midges is thought to have played a role in the spread of bluetongue virus in the Mediterranean basin and Northern Europe, and wind dispersal of infected mosquitoes is implicated in the spread of Japanese encephalitis virus to Australia (Kay and Farrow 2000; Ritchie and Rochester 2001; Carpenter et al. 2009). Infected vectors can also travel on their hosts, such as ticks (Dietrich et al. 2011) and Hippoboscid flies found on seabirds, but in such cases it is hard to determine the relative importance of the host or the vector in parasite colonization.

3.2.2 Anthropogenic Introduction

Human activities have a continuously increasing impact on the environment in direct relation with their unique capacity to innovate and harvest natural resources. Human colonization has been followed by species extirpation since prehistoric times (Milberg and Tyrberg 1993). The introduction of invasive species and diseases by humans is a major cause of disturbance of natural communities around the globe, and islands have not been spared (Blackburn et al. 2004; Bellard et al. 2016). Parasite invasions of islands can originate from accidental transport of invasive hosts and vectors (Wyatt et al. 2008), or the deliberate introduction of domestic animals (Bunbury et al. 2008) and game (Diamond and Veitch 1981). Probably one of the most famous examples of the impact of introduced parasites on insular wildlife is the decline of the Hawaiian endemic avifauna following the introduction of the avian malaria *Plasmodium relictum,* avianpox virus, and their mosquito vector *Culex quinquefasciatus* (Warner 1968; van Riper et al. 1986, 2002). In some rare cases, parasites are deliberately introduced in new areas as a mean to control invasive species. The most notorious example is the introduction of myxoma virus in Australia in the 1950s to control invasive rabbit populations (Fenner et al. 1957).

The globalization of human activities in the last decades has multiplied the risks of parasite emergence to an unprecedented scale (Daszak et al. 2000; Jones et al. 2008). The ever-expanding air transport network has dramatically increased the risk of global epidemics by facilitating the movement of infected hosts and disease vectors (Mangili and Gendreau 2005; Tatem et al. 2006a, b). Commercial ships have also contributed to the spread of many invasive species, including parasites and disease vectors across the globe (Ruiz et al. 2000; Lounibos 2002).

Habitat destruction and intensification of agriculture have also led to human encroachment into wildlife habitat and loss of biodiversity, increasing the risk of pathogen spill-over between humans, domestic animals, and wildlife (Daszak et al. 2001; Keesing et al. 2010). Due to their isolation and high level of endemism, species on oceanic islands are especially at risk in the face of these modern challenges (Kier et al. 2009; Bellard et al. 2016). Again we can refer to the example of Hawaii, where human activities have permitted secondary introduction of different strains of *Culex quinquefasciatus* in the archipelago, which has been associated with an increase in the altitudinal range of the mosquito and in malaria virulence, further increasing the impact of the disease on the endemic fauna (Fonseca et al. 2000, 2006).

3.2.3 Establishment After Arrival

The ecological processes associated with island colonization by hosts and parasites, such as the island syndrome and host switching, will be the subjects of Chaps. 4–7. Here, we will briefly mention some key factors influencing the success of parasite establishment in island communities.

Parasite colonization fundamentally depends on host colonization success (see Chap. 2), and on availability of suitable native hosts. During host colonization, the probability of parasite establishment and co-evolution with their host will also depend on parasite transmission efficiency. Parasites will have a higher risk of extinction when founding host populations are small, when stochastic events result in host extinction, and sometimes, when the host population front moves faster than the disease transmission front (Bar-David et al. 2006; MacLeod et al. 2010).

Parasite colonization will also depend on introduction effort, also called propagule pressure (Lockwood et al. 2005). Parasite establishment is more likely in situations where there are larger numbers of individual parasites arriving to the new area and more numerous arrival events. For parasites, introduction effort can be measured at the level of host individuals, populations, or species (Poulin 2004). Notably, parasites in aggregated distributions among few hosts are more susceptible to “missing the boat” and going extinct (Paterson et al. 1999; MacLeod et al. 2010). If its host fails to establish, parasites go extinct with them, unless other suitable hosts are present. Large and dense breeding colonies of seabirds are good host candidates for parasites because they provide a large number of potential hosts and regular opportunities of transmission (McCoy et al. 2016).

In comparison to continental species, endemic insular species may have a lower diversity of evolved immune defenses, probably as a consequence of their reduced parasite assemblages, which can increase their susceptibility to arriving parasites (Frankham 1997; Matson 2006). Infecting naive hosts allows parasites to remain in the new ecosystem even if the original, colonizing host goes extinct or is only transient (Smith and Carpenter 2006). Therefore, the capacity of the parasite to infect a wide range of hosts contributes greatly to its persistence after colonization. It has been argued that all parasites, except true specialists, can switch hosts rapidly if they can exploit newly available resources without having to evolve novel capacities (Hoberg and Brooks 2008). Lower prevalence and smaller distributions of host-specific avian blood parasites in island systems compared to widespread host-generalists provide support for this idea (Beadell et al. 2004; Ewen et al. 2012; Clark and Clegg 2015).

For vector-borne parasites, parasite establishment will also depend on the presence of a suitable vector. Parasites with high vector specificity have more restricted ranges than parasites with a wide range of vectors (Ishtiaq et al. 2010). Other important factors are vector habitat preferences, host specificity, and dispersal capacity (Ishtiaq et al. 2010). For this reason, the study of insular vector populations is critical to understand vector-borne parasite colonization.

3.3 Natural Parasite Colonization in the Galapagos Archipelago

Based on data compilations by Deem et al. (2011), Parker et al. (2006), and Sari et al. (2013), a total of 147 species of parasites and disease vectors have been identified in the Galapagos archipelago (see Table 3.2, Fig. 3.1). Of those, 95 could have arrived naturally, based on taxonomic or phylogenetic data, and their distribution in the native fauna. Most of these natural colonizations are directly transmitted parasites or arthropod disease vectors, although a relatively large number of native vector-borne blood parasites have been identified (see Fig. 3.1). These numbers are unlikely to accurately reflect the absolute or relative abundance of native and introduced parasites, as some host-parasite systems have been more heavily studied than others (e.g., parasites of the Galapagos avian fauna).

3.3.1 Colonization with a Vertebrate Host

In Galapagos, there are several examples of parasites that have naturally colonized the islands with their hosts (see Table 3.2). These are obligate parasites that are commonly found in close association with their bird hosts, usually with high prevalence and high densities on any given host. This happens because when hosts colonize a new area, less common parasites may have a higher chance of "missing the boat" (Paterson et al. 1999). Feather mites (Acari: Astigmata), lice (Insecta: Phthiraptera), and blood parasites (Apicomplexa: Haemosporida) represent good examples of colonizers that arrived to Galapagos with their vertebrate host. In order to make inferences about parasite arrival, we need to study the parasites from Galapagos animals and from their closest related continental species, which requires an understanding of the colonization history of the hosts themselves (see Chap. 2).

Table 3.2 Parasites recorded in the Galapagos Islands and their likely mode of arrival

Species	Type	Known host in Galapagos	Likely mode of arrival
Natural colonization			
Vector-borne parasites			
Myialges caulotoon	Mite	Galapagos hawk, flightless cormorant	Colonizing or migrating birds
Und. *Haemoproteus* spp. (8)[a]	Protozoa	Swallow-tailed gull, Galapagos dove,	Colonizing or migrating birds
		Frigatebird spp., Nazca booby	
Und. Microfilaria[a]	Nematode	Flightless cormorant, Galapagos penguin	Colonizing or migrating birds
Und. *Parahaemoproteus*	Protozoa	Blue-footed booby	Colonizing or migrating birds
Und. *Plasmodium* spp. (3)	Protozoa	Galapagos penguin	Migrating birds
Und. *Trypanosoma* sp.[a]	Protozoa	Galapagos hawk	Colonizing birds
Directly-transmitted parasites and mites			
Amerodectes atyeoi	Mite	Darwin's finches	Colonizing birds
Analges spp. (4)	Mite	Galapagos mockingbird spp.	Colonizing birds
Antartophtirus microchir	Louse	Galapagos sea lion	Colonizing or migrating mammals
Austrogoniodes demersus	Louse	Galapagos penguin	Colonizing or migrating birds
Atractis marquezi[a]	Nematode	Galapagos tortoise	Colonizing reptiles
Brueelia spp. (3)	Louse	Most passerines	Colonizing or migrating birds
Chlamydophila psittaci	Bacteria	Galapagos penguin, flightless cormorant, Galapagos dove	Colonizing or migrating birds
Colpocephalum spp. (3)	Louse	Galapagos hawk, Magnificent and Great frigate birds	Colonizing or migrating birds
Columbicola macrourae	Louse	Galapagos dove, Galapagos hawk	Colonizing or migrating birds
Contracecum sp.	Nematode	Brown pelican	Colonizing or migrating birds
Craspedorrhynchus sp.[a]	Louse	Galapagos hawk	Colonizing birds
Degeeriella regalis	Louse	Galapagos hawk	Colonizing birds
Dermanyssus sp.	Mite	Small ground finch	Colonizing birds
Dermoglyphus sp.	Mite	Darwin's finches	Colonizing birds
Eidmanniella albescens	Louse	Boobies	Colonizing or migrating birds
Fregatiella aurifasciata	Louse	Magnificent and great frigatebirds	Colonizing or migrating birds

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Eimeria spp. (2)	Protozoa	Galapagos reptiles	Colonizing reptiles
Eimeria palumbi[a]	Protozoa	Galapagos dove	Colonizing birds
Isospora spp. (6)[a]	Protozoa	Darwin's finches.	Colonizing birds
Isospora insularius[a]	Protozoa	Galapagos reptiles	Colonizing reptiles
Mesalgoides geospizae	Mite	Darwin's finches	Colonizing birds
Menacanthus distinctus[a]	Louse	Galapagos flycatcher	Colonizing birds
Myrsidea spp. (3)	Louse	Darwin's finches, Galapagos mockingbirds.	Colonizing birds
		Yellow warbler	
Nycteridocaulus sp.[a]	Mite	Galapagos flycatcher	Colonizing birds
Orthohalarachne diminuata	Mite	Galapagos sea lion	Colonizing or migrating mammals
Pectinopygus spp. (6)	Louse	Flightless cormorant, boobies, Frigatebirds	Colonizing or migrating birds
Philophthalmus zalophi[a]	Trematode	Galapagos sea lion	Colonizing or migrating mammals
Philopterus insulicola	Louse	Galapagos vermillon flycatcher	Colonizing birds
Physconelloides galapagensis[a]	Louse	Galapagos dove, Galapagos hawk	Colonizing or migrating birds
Piagetiella sp.	Louse	Brown pelican	Colonizing or migrating birds
Polysporella genovesae[a]	Protozoa	Galapagos mockingbirds	Colonizing birds
Natural colonization (continued)			
Directly-transmitted parasites and mites (continued)			
Proctophyllodes darwinii[a]	Mite	Darwin's finches	Colonizing or migrating birds
Renicola sp.	Trematode	Brown pelican	Colonizing or migrating birds
Ricinus marginatus[a]	Louse	Galapagos flycatcher	Colonizing birds
Strelkoviacarus spp.[a]	Mite	Darwin's finches	Colonizing or migrating birds
Trouessartia spp. (2)[a]	Mite	Small ground finch, Galapagos flycatcher	Colonizing birds
Tyrannidectes berlai[a]	Mite	Galapagos flycatcher	Colonizing birds
Xolalges palmai	Mite	Darwin's finches	Colonizing or migrating birds
Zonorchis meyeri[a]	Trematode	Galapagos rail	Colonizing birds
Disease vectors			
Aedes taeniorhynchus[a]	Fly	Multiple reptiles, mammal, and avian species	Direct colonization

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Amblyomma spp. (2[a] + 3)	Tick	Marine iguana, Galapagos tortoise, land iguana	Colonizing reptiles
Icosta spp. (2)	Fly	Galapagos hawk, flightless cormorant	Colonizing or migrating birds
Microlynchia galapagoensis[a]	Fly	Galapagos dove, mockingbrid spp.	Colonizing birds
Olfersia spp. (3)	Fly	Frigatebirds, flightless cormorant	Colonizing or migrating birds
Ornithodoros spp. (2[a] + 1)	Tick	Marine iguana, Galapagos tortoise, land iguana	Colonizing reptiles
Ornithoica vicina	Fly	Unknown	Colonizing or migrating birds
Tabanus vittiger[a]	Fly	Multiple reptiles, mammal, and avian species	Direct colonization
Vatacarus spp. (3)	Tick	Marine iguana, waved albatross	Colonizing reptiles and birds
Anthropogenic colonization			
Vector-borne parasites			
Avipoxvirus (canarypox)	Virus	Galapagos finches, Galapagos mockingbird, Yellow warbler	Introduced or migrating birds
Avipoxvirus (fowlpox)	Virus	Chicken	Introduced chicken
Dirofilaria immitis	Nematode	Galapagos sea lion, dog	Introduced dogs
Directly-transmitted parasites			
Ancylostoma caninum	Nematode	Dog	Introduced dogs
Ascaridia galli	Nematode	Chicken	Introduced chicken
Avian *Adenovirus*	Virus	Chicken, Galapagos finches, waved albatross	Introduced chicken
Avian *Birnavirus*	Virus	Chicken	Introduced chicken
Avian *Coronavirus*	Virus	Chicken	Introduced chicken
Avian encephalomyelitis virus	Virus	Chicken	Introduced chicken
Avian P*aramyxovirus* 1	Virus	Chicken, Galapagos finches	Introduced chicken
(Newcastle virus)			
Bartonella spp.	Bacteria	Dog	Introduced dogs
Bovicola spp.	Louse	Goat, Galapagos hawk	Introduced goat
Canine *Adenovirus*	Virus	Dog	Introduced dogs
Canine *Coronavirus*	Virus	Dog	Introduced dogs

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Canine distemper virus	Virus	Dog	Introduced dogs
Canine parainfluenza virus	Virus	Dog	Introduced dogs
Canine *Parvovirus*	Virus	Dog	Introduced dogs
Capillaria sp.	Nematode	Chicken	Introduced chicken
Anthropogenic colonization			
Directly-transmitted parasites (continued)			
Cryptosporidium sp.	Protozoa	Dog	Introduced dogs
Davainea proglottina	Cestode	Chicken	Introduced chicken
Dispharynx sp.	Nematode	Chicken	Introduced chicken
Ehrlichia/Anaplasma spp.	Bacteria	Dog	Introduced dogs
Epidermoptes bilobatus	Mite	Chicken	Introduced chicken
Feline *Herpesvirus*	Virus	Cat	Introduced cats
Feline *Calicivirus*	Virus	Cat	Introduced cats
Gallid *Herpesvirus* (2) (Marek's disease)	Virus	Chicken	Introduced chicken
Gammacoronavirus	Virus	Chicken	Introduced chicken
Giardia sp.	Protozoa	Dog	Introduced dogs
Isospora canis	Protozoa	Dog	Introduced dogs
Leishmania donovani	Protozoa	Dog	Introduced dogs
Macrorhabdus sp.	Bacteria	Chicken	Introduced chicken
Mycoplasma gallisepticum	Bacteria	Chicken	Introduced chicken
Mycoplasma haemocanis	Bacteria	Dog	Introduced dogs
Mycoplasma haemofelis	Bacteria	Dog	Introduced dogs
Avian *Orthoreovirus*	Virus	Chicken	Introduced chicken
Oxyspirura mansoni	Nematode	Chicken	Introduced chicken
Papillomavirus bovino	Virus	Cattle	Introduced cattle
Feline panleukopenia virus	Virus	Cat	Introduced cats
Philornis downsi	Fly	Galapagos finch, flycatcher, mockingbird spp.	Human transport stowaway
Raillietina echinobothrida	Cestode	Chicken	Introduced chicken
Sarcocystis canis	Protozoa	Dog	Introduced dogs
Sarcodexia lambens	Fly	Darwin finch spp.	Human transport stowaway, Introduced birds
Tetrameres sp.	Nematode	Chicken	Introduced chicken
Toxocara canis	Nematode	Dog	Introduced dogs
Toxoplasma gondii	Protozoa	Cat, Galapagos penguin, cormorant	Introduced cats
Trichomonas gallinae	Protozoa	Rock dove, Galapagos dove	Introduced rock doves
Wolbachia pipiens	Bacteria	Dog	Introduced dogs

(continued)

Table 3.2 (continued)

Species	Type	Known host in Galapagos	Likely mode of arrival
Disease vectors			
Aedes aegypti	Fly	Human	Human transport stowaway
Culex quinquefasciatus	Fly	Mammals and birds	Human transport stowaway
Culicoides pusillus	Fly	Mammals	Human transport stowaway
Simulium punctatum	Fly	Humans	Human transport stowaway

This list is based on compilations done by Deem et al. (2011), Parker et al. (2006), and Sari et al. (2013). The type « fly » includes insects of the order Diptera, and the type « louse » regroups insects of the order Phthiraptera. “Und”, undescribed species. Numbers between brackets in front of species names indicates the number of species identified

[a] Species confirmed to be native by taxonomic or phylogenetic studies

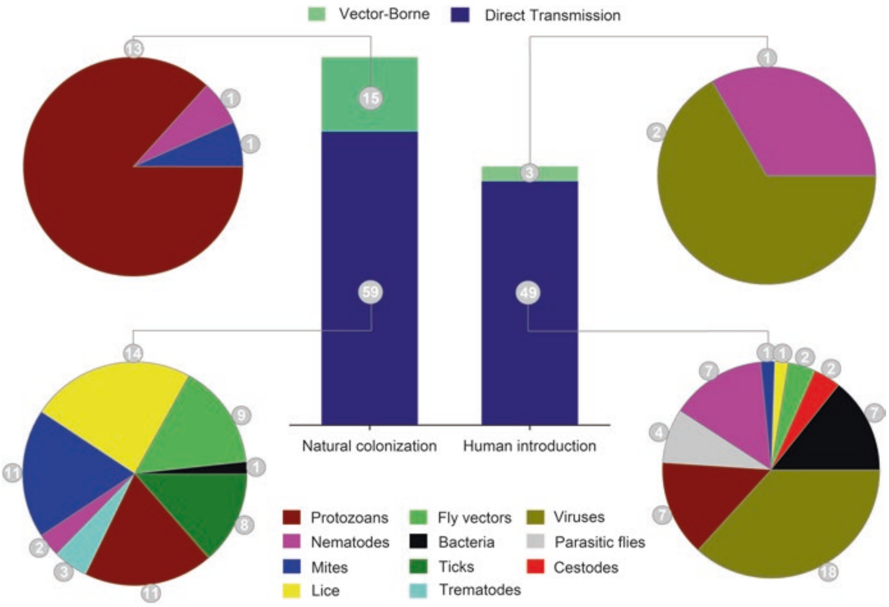

Fig. 3.1 Graphical representation of the number and different types of parasites and vectors identified in the Galapagos Islands

3.3.1.1 Co-colonization of Hosts and Parasites: Examples from Lice and Mites on the Galapagos Flycatcher and the Galapagos Hawk

The Galapagos flycatcher (*Myiarchus magnirostris*) colonized the Galapagos Islands about 850,000 years ago, and their closest relatives are the Brown-crested flycatchers (*Myiarchus tyrannulus*) from Central America (Sari and Parker 2012). In order to investigate which parasites colonized the archipelago with their hosts, Sari et al. (2013) sampled mites, lice, and blood parasites from Galapagos flycatchers on seven Galapagos islands and also from Brown-crested flycatchers at four locations in Costa Rica. These authors described a suite of six mite and louse species infecting Galapagos flycatchers, of which five species are shared with the Brown-crested flycatchers, leading to the conclusion that these mites and lice arrived to Galapagos together with their bird hosts when they naturally colonized the archipelago. Taking a closer look at the morphology of this ectoparasite assemblage, Sari et al. (2013) reported that only one of these species, a mite from the genus *Nycteridocaulus* (Family Proctophyllodidae), has evolved evident morphological differentiation between the two host species, leading to the conclusion that the *Nycteridocaulus* from the Galapagos flycatcher is probably not conspecific with that from the Brown-crested flycatcher. The other mite and louse species have the same morphological characteristics and taxonomic classification, for both host species. However, genetic distance between *Ricinus marginatus* lice collected from both host species was found to be almost ten times larger than the genetic distance between their hosts (Sari et al. 2013). Both hosts and their lice have been evolving in allopatry for about 850,000 years (see Chap. 2), but evident speciation was only observed in the bird hosts (Sari et al. 2013). These findings add to the body of knowledge indicating that morphological evolution tends to be more conservative in parasites than their hosts (Klassen 1992) and suggest that the process of speciation for lice can take much longer than it takes for their hosts, as mentioned by McDowall (2000).

A similar pattern was also observed for the Galapagos Hawk (*Buteo galapagoensis*) (Whiteman et al. 2007, 2009), a more recent arrival to Galapagos than the Galapagos flycatcher. The Galapagos hawk colonized the archipelago about 300,000 years ago and its closest related continental species is the Swainson's Hawk (*Buteo swainsoni*) (Bollmer et al. 2006; Amaral et al. 2009) (see Chap. 2). Five species of ectoparasites have been found on hawks on several of the Galapagos islands: one hippoboscid fly (*Icosta nigra*), three species of lice (*Degeeriella regalis*, *Colpocephalum turbinatum*, and *Craspedorrhynchus* sp.), and one skin mite (*Myialges caulotoon*) (Whiteman et al. 2006, 2007, 2009). All these species are also found on Swainson's hawks and are thought to have colonized Galapagos together with their hawk host (Price et al. 2003; Parker et al. 2006). Whiteman et al. (2009) looked at variation in both morphology and DNA sequences for one of these species, the head louse *Craspedorrhynchus* sp., in populations of Galapagos hawks and Swainson's hawks in North and South America. They found approximately 10% genetic divergence between lice from the two host species, while almost no genetic differentiation was found between the Galapagos and the Swainson's hawks used in this study (only one base pair in 497 nucleotides sequenced of COI). In contrast, hawks from Galapagos and Swainson's hawks are strikingly different in morphology but the *Craspedorrhynchus* lice found on the two hosts showed a lot of overlap in morphological characteristics. Subtle morphological differences, however, were observed in the head and genitalia of lice between the two host species, allowing the identification of their geographical origin and possibly lineage diversification.

Parasites that colonized the Galapagos with their vertebrate hosts share patterns of distribution and evolutionary history with their hosts. Rivera-Parra et al. (2015) showed that the species identity of the host was more important than sampling location for determining the phylogenetic relationships within each species of louse parasitizing two related seabird species, despite the fact that the hosts breed together in dense mixed-species colonies. However, these lice have different prevalence on different islands, demonstrating that the relationships among parasites, hosts, and islands are idiosyncratic (Rivera-Parra et al. 2014). Nematode parasites that colonized Galapagos together with the founding population of the Galapagos tortoises (*Chelonoidis nigra* species complex) also show a similar island-dependent distribution (Fournié et al. 2015). Each Galapagos tortoise species is found only on one island, and each island has a different combination of nematodes. Fournié et al. (2015) suggested that the observed pattern could have resulted from a neutral process of founder events following the arrival of tortoises to Galapagos.

3.3.1.2 The Potential Role of Migratory Birds in Parasite Colonization: The Arrival of *Plasmodium* (Avian Malaria) to Galapagos

Parasites might also colonize the Galapagos archipelago via migratory or vagrant birds. For example, *Plasmodium* parasites detected in Galapagos endemic passerine bird species may have arrived with migratory Bobolinks (*Dolichonyx oryzivorus*; see Fig. 3.2) (Levin et al. 2013). Four lineages of *Plasmodium* parasites have been identified in the Galapagos (Levin et al. 2009, 2013). One lineage was repeatedly detected in Galapagos penguins and occasionally in yellow warblers and the other three were only detected in one or a handful of Galapagos birds at one location, at one given time (Levin et al. 2013). A very large sampling effort (nearly 4000 birds molecularly screened for blood parasites) was needed in order to reveal these few rare lineages. Interestingly, two of the rare lineages were perfect DNA matches with *Plasmodium* lineages amplified from North American breeding bobolink samples (Levin et al. 2013). Although this is not confirmation that migratory bobolinks introduced these rare lineages to the Galapagos, it is evidence that the islands may be exposed to more potential parasite introductions than previously thought. It is not currently known whether these rare lineages have established in the islands.

Because bobolinks spend time in both the southern and northern hemispheres during mosquito breeding season, they probably acquire blood parasites in both locations. By comparing the blood parasites found in North American breeding bobolinks to those found in the brown-headed cowbird, a short-distance migrant that breeds in sympatry, the authors were able to begin teasing apart the potential origins of the rare Galapagos *Plasmodium* lineages (Levin et al. 2016). If the Galapagos *Plasmodium* lineage is shared between bobolinks and cowbirds and pre-

Fig. 3.2 Picture of Bobolink (*Dolichonyx oryzivorus*) captured in Galapagos (Photo: Jenn Megyesi)

dominantly matches DNA sequences from other North American hosts, the colonizing lineage is likely of North American origin. If this lineage is detected in bobolinks but not cowbirds and matches predominantly South American sequences, then the origin is mostly likely South American. Bobolinks stop over in Galapagos only during their southward migration, but could still harbor chronic infections by parasites acquired many months before, while overwintering. Indeed, one of the *Plasmodium* lineages found in Galapagos birds was likely of North American origin, while the other match was likely from South America (Levin et al. 2016). More work is needed to further understand the probability of colonization by blood parasites (and other parasites) via migratory birds. Recently, several bobolinks have been sampled in Galapagos in October during migration (P. Parker, personal communication). By far the most abundant migratory birds in Galapagos are shorebirds, and to our knowledge, none have been tested for blood parasites.

3.3.2 Colonization with/of Vectors

Multiple blood-feeding arthropods with the capacity to disperse and transmit parasites may have naturally colonized the Galapagos archipelago (see Table 3.2, Fig. 3.1). In all the cases, we have little knowledge of either their origin and native status, or their exact role as disease vectors in Galapagos. The origin and phylogenentic relationships of the only mosquito native to the Galapagos Islands, *Aedes taeniorhynchus,* are probably the best studied (Bataille et al. 2009a), although its role as a disease vector is still not clear. Conversely, the role of Hippoboscid flies (four genera and seven species in Galapagos; see Table 3.2 and Fig. 3.1) in the transmission of avian blood parasites has been well studied (Valkiunas et al. 2010; Levin et al. 2011, 2012), but their origin is uncertain. These two contrasting cases will be explored further below.

Two ticks of the genus *Ornithodoros* infecting reptiles are endemic to the Galapagos Islands (Wikelski 1999). Two other *Amblyomma* and three *Vatacarus* ticks parasitizing reptiles and one avian *Ornithodoros* species are also found in the archipelago and probably arrived naturally with their hosts. All these arthropods could be involved in the transmission of *Hepatozoon* parasites, mainly through ingestion by the vertebrate host (Smith 1996; Bataille et al. 2012). One horse-fly species of the genus *Tabanus* has also been classified as endemic to Galapagos (Sinclair 2017) and can feed on Galapagos reptiles (Philip 1976, 1983), but its role in disease transmission is completely unknown.

As argued in the introduction of this chapter, it is hard to determine whether a native vector, a native host, or both brought a colonizing parasite to Galapagos (see Sect. 3.1). Combined phylogenetic studies of parasite, vector, and host may help resolve this issue. This type of study has been carried out with mites vectored by hippoboscid flies and infecting endemic Galapagos birds (Whiteman et al. 2006), although this study focused on parasite population structure and host specificity rather than on their origin (see Chap. 8).

3.3.2.1 The Black Salt Marsh Mosquito (*Aedes taeniorhynchus*): A Successful Endemic Vector with Unclear Role in Galapagos Disease Ecology

Aedes taeniorhynchus is widely distributed in temperate and tropical coastal areas of the New World (Lang 2003). It breeds primarily in temporary-water habitats, producing huge broods after flood or heavy rains. The species is widely distributed across the Galapagos Islands. The presence of *A. taeniorhynchus* in the archipelago was first recorded in the late 1880s (Howard 1889). It was suggested early on that *A. taeniorhynchus* might have naturally reached the archipelago before the arrival of humans (Hardy 1960). On the other hand, pirates and later whalers frequently visited the archipelago between the sixteenth and nineteenth centuries, giving multiple opportunities to introduce *A. taeniorhynchus.*

To tackle this question, Bataille et al. (2009a) performed phylogenetic analyses using mitochondrial and nuclear DNA markers on *A. taeniorhynchus* specimens collected across the Galapagos archipelago and across the species' continental range. All analyses placed the Galapagos population of *A. taeniorhynchus* within one single coherent cluster clearly separated from the continental mosquito populations. This result suggests that the Galapagos population of *A. taeniorhynchus* originated from a single colonization event and now represents a distinct evolutionary unit divergent from the continental populations. Molecular clock analysis estimated that the Galapagos and continental clades diverged 176,000 years ago (95% confidence interval: 93,000–352,000 years). Although imprecise, this estimation demonstrated that the colonization by *A. taeniorhynchus* was not human-driven.

Some characteristics of the biology of *A. taeniorhynchus* support the hypothesis that this mosquito had the capacity to naturally colonize the Galapagos Islands and successfully establish itself across the archipelago. First, the strong flying capacity of *A. taeniorhynchus* is well known, and long-distance dispersal has been observed various times in this species (Provost 1951; Bello et al. 2005). Arrival of *A. taeniorhynchus* in Galapagos could have been facilitated by the strong wind and oceanic current found in the Intertropical Convergence Zone during cyclic climatic fluctuations such as El Niño events (Peck 1994). Second, *A. taeniorhynchus* lays desiccation-resistant eggs, which has been significantly associated with the success of invasive mosquito introductions in new areas (Juliano and Lounibos 2005). Third, larvae of *A. taeniorhynchus* successfully grow in water with a wide range of salinity (Clark et al. 2004), which gives them the possibility to breed in a wide range of habitats across the archipelago, notably in the mangroves found throughout the coasts of the archipelago.

The role of *Aedes taeniorhynchus* as a disease vector in Galapagos is still poorly understood, but is likely to be important (see Fig. 3.3). This species has a wide distribution, high population density, and strong dispersal capacity (Bataille et al. 2010, 2011) (see Chap. 8), so it represents an ideal vector for native and invasive mosquito-borne parasites. Moreover, it feeds opportunistically on a wide range of vertebrate hosts including birds, mammals, and reptiles (Bataille et al. 2012). This species could thus act as a bridge vector across most of Galapagos endemic wildlife (Kilpatrick et al. 2005).

Swarms of mosquitoes can be an important nuisance for Galapagos wildlife. For example, waved albatrosses (*Phoebastria irrorata*) on Española island were observed deserting their nests and neglecting their eggs due to mosquito harassment (Anderson and Fortner 1988). *Aedes taeniorhynchus* is a competent vector for the transmission of various viruses, including West Nile virus (Hardy et al. 1984; Turell et al. 1994, 2001), but, fortunately, none of those are currently present in the archipelago. *Aedes taeniorhynchus* is also considered an important vector of the dog heartworm (*Dirofilaria immitis*) (Labarthe et al. 1998; Labarthe and Guerrero 2005). The disease was introduced with dogs in Galapagos Islands (Levy et al. 2008), but the role of *A. taeniorhynchus* in its transmission, notably to Galapagos sea lions and fur seals (Dunn and Wolke 1976, Sato et al. 2002), has not been verified.

PCR-based parasite screening identified the presence of *Haemoproteus* parasites and of microfilarial nematodes in pools of mosquito thoraces collected in Fernandina and Isabela Islands (Bataille et al. 2012). However, these results do not provide direct evidence for the role of *A. taeniorhynchus* in the transmission of these parasites. Mosquitoes are not the typical vectors of *Haemoproteus* spp., although some studies have supported this possibility (Ishtiaq et al. 2008). Galapagos microfilarial nematodes infect the flightless cormorants and the

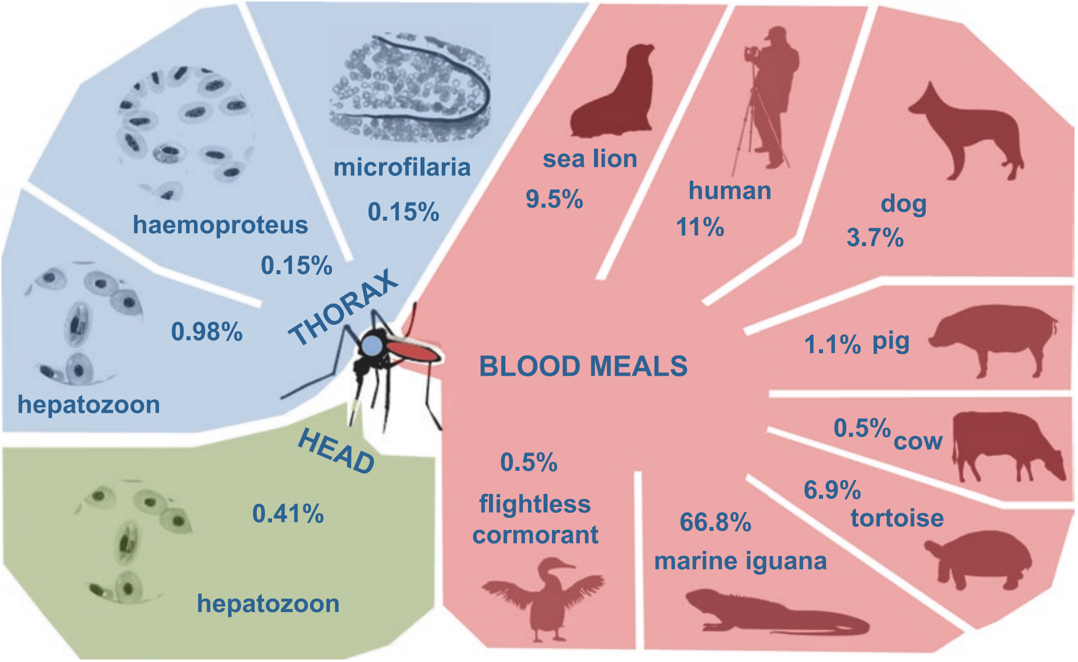

Fig. 3.3 Blood-feeding patterns and parasite infection rates in pools of thoraces and heads of the black salt marsh mosquito (*Aedes taeniorhynchus*) in Galapagos (from Bataille et al. 2012)

Galapagos penguins (Merkel et al. 2007). They may be transmitted by multiple vector species, but *Aedes taeniorhynchus* is thought to be one important vector for this parasite, because microfilariae prevalence across its hosts' ranges correlates with ecological factors suitable for *A. taeniorhynchus* populations (Siers et al. 2010), and this mosquito was shown to feed on cormorants (Bataille et al. 2012). *Hepatozoon* parasites were also detected by PCR in both thoraces and heads of mosquitoes. *Aedes taeniorhynchus* could be involved in the transmission of this parasite by accidental ingestion of infected mosquitoes, but maybe also by mosquito bites (Telford et al. 2001). This mosquito could also be a mechanical vector (i.e., transfer of the parasite without passage within the vector necessary for the parasite's life cycle) of avipoxvirus between birds in the archipelago (Thiel et al. 2005).

3.3.2.2 Hippoboscid Flies (Hippoboscidae): Vectors of Unclear Origin with an Important Role in Blood-Parasite Transmission

Hippoboscid flies are obligate, blood-feeding ectoparasites found on birds and mammals. Although some are wingless (e.g., sheep ked), most hippoboscids have fully functional wings. Despite the ability to fly, hippoboscids tend to remain closely associated with their hosts, with only one off-host life stage: female hippoboscids lay a single, late-instar larva, which pupates in the ground. Hippoboscid flies are common on Galapagos seabirds, the Galapagos hawk, and the Galapagos dove (Whiteman et al. 2007; Valkiunas et al. 2010; Levin et al. 2012) (see Fig. 3.4). The flies tend to be very host-specific, with one fly species per host species (or a few closely related host species). For example, over the course of sampling >100 flies from great and magnificent frigatebirds and blue-footed, red-footed, and Nazca boobies, the species of hippoboscid that infects boobies, *Olfersia aenescens*, was never found on a frigatebird and vice versa, despite the fact that these seabirds often breed in dense, multi-species colonies with ample opportunity for flies to host-switch (I. Levin, personal observation.). Hippoboscid flies are definitive hosts for

Fig. 3.4 Hippoboscid fly on a Nazca booby (*Sula granti*; photo: Iris I. Levin)

blood parasites in the subgenus *Haemoproteus haemoproteus* (Valkiunas 2005; Levin et al. 2011). Because of the host-specificity of the flies, lineages of *H. haemoproteus* are often specific to a particular host and fly pair (Valkiunas et al. 2010; Levin et al. 2011, 2012).

For reasons already mentioned, it is difficult to determine the order and combination of arrival in Galapagos: did colonizing birds arrive infected with flies and *Haemoproteus*? Or did the flies and *Haemoproteus* arrive later? Perhaps the most parsimonious explanation is that colonizing birds were infected with both parasite and vector, but we have little evidence to back up this claim. The various DNA lineages of *Haemoproteus multipigmentatus* found infecting Galapagos doves were also detected in continental South American dove species (Santiago-Alarcon et al. 2010). These lineages do not appear to have diversified recently from one single lineage, which would be evidence of differentiation within the Galapagos archipelago since arrival. Instead, it seems plausible that this parasite was introduced recently and multiple times to Galapagos, probably via a vagrant dove host like the eared dove (*Zenaida auriculata*) or with introduced rock doves, both of which have been found to be hosts of *H. multipigmentatus* (Santiago-Alarcon et al. 2010; Valkiunas et al. 2010). Rock doves were introduced to Galapagos in the early 1970s and are now completely eradicated from the islands, but *H. multipigmentatus* was also detected in rock doves once collected in Galapagos (P. Parker, personal communication). Interestingly, rock doves in continental areas are infected with the hippoboscid fly *Pseudolynchia canariensis*, while the flies found infecting Galapagos doves belong to the species *Microlynchia galapagoensis*, so the role of the supposed vector of *H. multipigmentatus* in Galapagos in these multiple colonization events is currently unknown.

In contrast, Galapagos frigatebird species are infected with just one lineage of *Haemoproteus iwa*, which is probably vectored by the hippoboscid fly, *Olfersia spinifera* (Levin et al. 2011). Vector confirmation for both *M. galapagoensis* and *O. spinifera* involved DNA amplification of *Haemoproteus* from fly thorax without amplification of avian host DNA, indicating developing parasite (sporozoite) in the thorax (Valkiunas et al. 2010; Levin et al. 2011). Although Galapagos frigatebirds are genetically isolated from frigatebirds in the rest of their tropical range (Hailer et al. 2010; see Chap. 2), only one *Haemoproteus iwa* lineage has ever been recovered both in Galapagos birds and frigatebirds in other locations (Levin et al. 2011). Magnificent frigatebirds colonized the Galapagos archipelago approximately 247,200 years ago (95% confidence intervals: 82,800–647,400) (Hailer et al. 2010). Using the estimated DNA sequence divergence rate for the hemosporidian cytochrome *b* gene (1.2% per million years, Ricklefs and Outlaw 2010), the lack of sequence divergence within Galapagos is consistent with the parasite and vector arriving with the colonizing host (Levin et al. 2011). However, it is still possible that the parasite and fly vector are more recent arrivals. Frigatebirds are philopatric to their breeding site, but travel great distances during the non-breeding season (Dearborn et al. 2003; Weimerskirch et al. 2006). We know that hippoboscid flies do regularly move between host individuals at a local scale; interestingly, the flies that do move between birds are less likely to be infected with *Haemoproteus iwa* (Levin and Parker 2014). In order to fully understand the colonization history of hippoboscid fly vectors in Galapagos, large-scale phylogenetic and phylogeographic studies of *Haemoproteus* parasites, bird hosts, and hippoboscid flies are needed, with an effort to estimate arrival dates where possible.

3.4 Anthropogenic Colonization

The introduction of new parasites and disease vectors due to human activities represents a major threat to Galapagos Islands biodiversity (Wikelski et al. 2004; Gottdenker et al. 2005; Whiteman et al. 2005; Kilpatrick et al. 2006b). This threat has substantially increased in the last two decades due to the rapid growth of the resident and visitor population associated with the booming tourism industry (Peck et al. 1998; UNESCO 2006; UNESCO 2010). As for isolated islands elsewhere, the principal routes of introduction of disease vectors and parasites to the Galapagos Islands are transport by boat and airplanes (Wikelski et al. 2004; Causton et al. 2006; Kilpatrick et al. 2006b).

There are two airports in Galapagos (Baltra and San Cristobal Islands) connecting the archipelago to Guayaquil and Quito in mainland Ecuador, and one cargo route from Guayaquil stopping at San Cristobal, Santa Cruz, and Isabela Islands (Fig. 3.5). Private jets have flown to Galapagos directly from places as varied as Florida, Brazil, and the Middle East without any systematic quarantine measures (Cruz Martinez and Causton 2007). In 2011, more than 2800 commercial flights, 200 cargo ships, and 400 privately-owned jets or boats made trips to the Galapagos Islands (Galapagos quarantine and inspection system-SICGAL annual report 2011). A quarantine and inspection system (SICGAL) is in place to control the movement of goods to and between islands (Causton et al. 2006), but presently SICGAL does

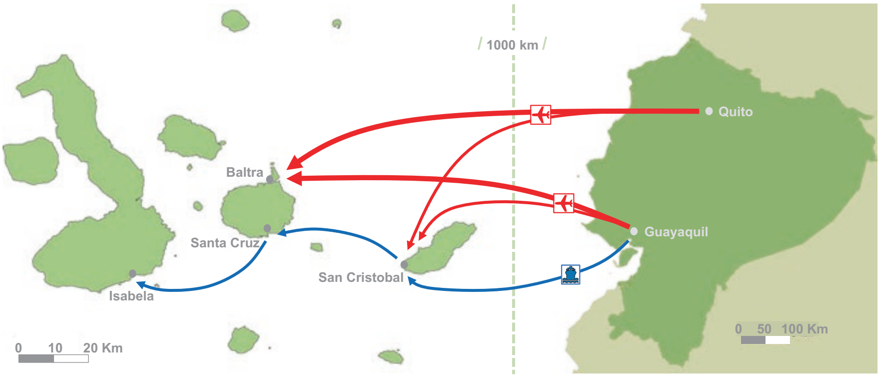

Fig. 3.5 Map showing shipping and air traffic routes connecting the Galapagos Archipelago to mainland Ecuador. Most flights (~70%, representing over 2000 flights a year) arrive at Baltra airport

not have the capacity to effectively implement the procedures that are necessary to prevent carriage of stowaway invertebrates by plane or boat to (and within) the Galapagos Archipelago (UNESCO 2006; UNESCO 2010).

Human activities have directly affected the health of the native Galapagos fauna through deliberate or accidental killing and injuries by humans or by other species they have introduced since the discovery of the archipelago (Dowler et al. 2000; Gottdenker et al. 2008; Poulakakis et al. 2008; Denkinger et al. 2015). Beyond physical injuries, human presence can also have a direct stress-related effect on the health of Galapagos wildlife. Notably, it has been shown that even low levels of human disturbance like ecotourism can increase levels of the stress hormone corticosterone in marine iguanas and modify some of their immune response capacities such as bacterial killing ability or cutaneous wound healing (French et al. 2010). In Galapagos sea lions, the immune activity and body condition of individuals living in the urban colony of Puerto Baquerizo Moreno on San Cristobal Island differ from those in the colonies located in the protected zones of the National Park (Brock et al. 2013). Human-related impact on this urban sea lion colony includes close contact with humans and domestic animals, contact with pollutants from sea vessels, and with bacteria of human origin (Wheeler et al. 2012; Brock et al. 2013; Denkinger et al. 2015).

Free-living, motile parasites that can survive a long time in the environment may have arrived directly to the Galapagos archipelago by hitchhiking on human transports. The parasitic botfly *Philornis downsi* represents the most likely case of such stowaway introduction in the archipelago. This fly lays eggs in bird nests and the larvae feed on blood of nestlings, with negative consequences on nestling survival (Fessl et al. 2006; Koop et al. 2011). *Philornis downsi* was introduced to the Galapagos Islands from mainland Ecuador in the 1960s (Causton et al. 2006; Bulgarella et al. 2015), maybe with imported fruit or in the cargo holds of planes. Alternatively, it could have been introduced with infected vertebrate hosts, for example chickens or pigeons, or with their nest material. The case of this fly and its impact on Galapagos avifauna will be discussed in detail in Chap. 9.

3.4.1 Colonization with Introduced Vertebrate Host

Most invasive parasites detected in the native Galapagos terrestrial vertebrate fauna probably originated from introduced vertebrate hosts, especially domestic animals. Parasites introduced with chickens have been particularly well studied. Several surveys carried out on chickens from inhabited islands of the archipelago (Gottdenker et al. 2005; Soos et al. 2008; Deem et al. 2012) indicated infection by *Mycoplasma gallisepticum*, a globally distributed bacterium that causes chronic respiratory disease in poultry and conjunctivitis in wild birds (Williams et al. 2002), and by nine different types of viruses, including the contagious Newcastle disease (avian paramyxovirus 1) that infects many domestic and wild avian species (Alexander et al. 2012). Antibodies to Newcastle virus and to an adenovirus

(Adenovirus-2) were also detected in Galapagos finches on Floreana Island, suggesting potential spillover from poultry to wild birds (Deem et al. 2012). Multiple nematode, cestode, trematode, and protozoan parasites were also identified, including a *Dyspharynx* nematode that has been associated with mortalities in Galapagos dark-billed cuckoos (Gottdenker et al. 2005). Marek's disease, caused by a herpesvirus, is also present and caused mortality in Galapagos domestic poultry in 1995/1996, but risks for native Galapagos avifauna are considered low because there are no susceptible native galliform species in the archipelago (Miller et al. 2001; Gottdenker et al. 2005).

Galapagos poultry are also infected by avian pox, caused by an avipoxvirus of the fowlpox lineage (Gottdenker et al. 2005). However, this strain of avipoxvirus seems restricted to chickens, whereas other strains of the canarypox lineage have been affecting the Galapagos passerine birds since at least 1899 (Thiel et al. 2005; Parker et al. 2006, 2011). This canarypox virus lineage can have a major impact on the survival of some endemic passerine populations during stressful environmental conditions like El Niño events (Curry and Grant 1989). Examination of museum specimens suggested that this avipoxvirus arrived to the archipelago in the late 1890s, possibly with early settlers, or via a natural colonization with migrating passerines like Bobolinks (see Sect. 3.2) (Parker et al. 2011). Despite the difference in hosts between fowlpox and canarypox viruses, the sympatry of the two pox lineages in some areas may allow for recombination and virulence alteration of avian pox viruses in Galapagos (Thiel et al. 2005). The transmission of avian pox in the archipelago is probably facilitated by endemic and introduced mechanical vectors (see sections on vectors above and below).

Importation of broiler chickens for industry in Galapagos increases the risk of introducing avian parasites to the archipelago. Strict biosecurity protocols are not implemented in Galapagos broiler houses, permitting direct contact of wild birds with poultry (Gottdenker et al. 2005). However, backyard chickens may represent a greater threat of disease spillover to Galapagos wildlife than broiler chicken, because they harbor more parasites and are more frequently in contact with wildlife (Soos et al. 2008).

Rock doves introduced to the Galapagos Islands facilitated the arrival of the flagellate protozoa *Trichomonas gallinae*, and the subsequent infection of Galapagos doves by this parasite (Wikelski et al. 2004). Domestic cats and dogs also brought their parasites with them to the Galapagos archipelago. High prevalence (20–60%) of canine distemper virus and the dog heartworm *Dirofilaria immitis* have been detected in Galapagos dog populations, which has led to major concerns of spillover to marine mammals (Levy et al. 2008; Diaz et al. 2016). Of the parasites infecting cats in Galapagos Islands, the high prevalence of *Toxoplasma gondii* represents the most significant threat to the endemic wildlife (Levy et al. 2008). This protozoan parasite infects all warm-blooded animals, including humans, but felid species are their only definitive hosts, necessary for their sexual reproduction (Tenter et al. 2000). Infected cats can notably transmit the parasite to other hosts via ingestion of contaminated feces. Infection by *T. gondii* was observed in many species of birds across the globe (Dubey 2002), including the endemic bird 'Alala from Hawaii

(Work et al. 2000). In Galapagos, low prevalence (1–8%) of antibodies to *T. gondii* was detected in Galapagos penguins and flightless cormorants (Deem et al. 2010).

Apart from the potential spread of parasites through the introduced domestic species, a few introduced species that now live in the wild could also have brought parasites to the Galápagos with them. The smooth-billed ani and the cattle egret are abundant birds in Galapagos that were brought by humans and could represent a source of new parasites, but they have not yet been well studied in this respect.

3.4.2 Anthropogenic Introduction of Vectors

Several disease vectors have been introduced by humans to the Galapagos archipelago, but, for most of them, the exact mode and frequency of introduction has not been studied in detail. The yellow fever mosquito, *Aedes aegypti,* has been present in urbanized areas of Santa Cruz and San Cristobal Islands since 2001, and is associated with cases of dengue fever since then (Causton et al. 2006). The biting midge *Culicoides pusillus,* a potential vector for blue tongue virus, is established in Santa Cruz Island since at least 1964 (Causton et al. 2006). The blackfly, *Simulium bipunctatum*, vector of the river blindness worm, was detected in 1989 and is distributed on three islands, including the uninhabited Santiago Island (Causton et al. 2006). Lastly, the southern house mosquito, *Culex quinquefasciatus*, vector of multiple parasites such as avian malaria parasites and West Nile virus, was first recorded in 1985 in Santa Cruz, and is now distributed in all inhabited islands of the archipelago (Peck et al. 1998; Causton et al. 2006).

All these vectors have restricted distribution in the archipelago because they require fresh water for breeding, which is mostly accessible in the humid areas of the islands and in human-inhabited areas, where open fresh water tanks and man-made cavities (e.g., discarded tires and containers) containing fresh water are readily available (Fig. 3.6). The only introduced disease vector that has been studied in further detail is *C. quinquefasciatus*.

3.4.2.1 The Southern House Mosquito (*Culex quinquefasciatus*): On-Going Introduction of a Major Disease Vector

Culex quinquefasciatus is a member of the globally distributed *Culex pipiens* species complex, and is found in tropical and sub-tropical regions where it breeds in freshwater with high organic content, depositing egg rafts on the water surface. It is extremely successful in human-inhabited areas because of the abundance of stagnant freshwater bodies, but it also breeds in forest environments. It is an important vector for a wide variety of diseases, such as West Nile virus (Sardelis et al. 2001), filariasis (Farid et al. 2001), avian pox and avian malaria (van Riper et al. 1986; Fonseca et al. 2000). It feeds readily on mammals and birds, so it can play the role of a bridge vector, notably for the transmission of West Nile virus (Sardelis et al.

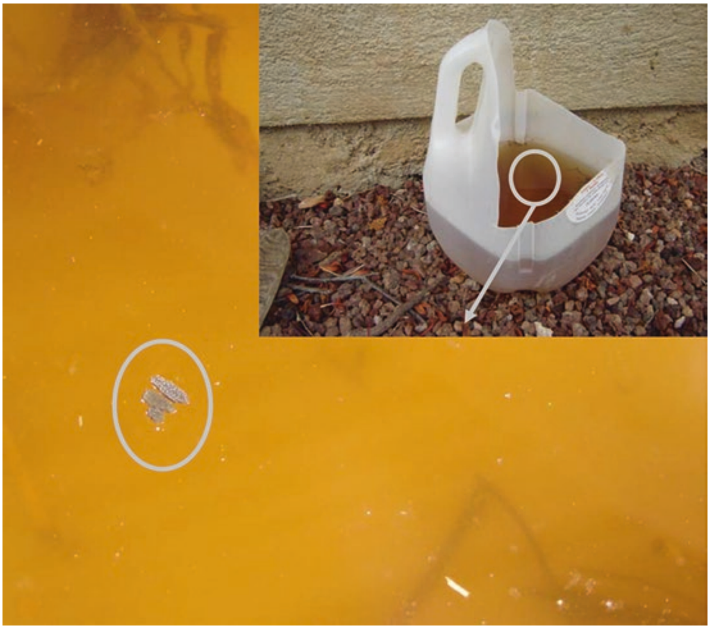

Fig. 3.6 Eggs of the introduced southern house mosquito (*Culex quinquefasciatus*) deposited in an abandoned plastic container filled with water (Photos: Arnaud Bataille)

2001). The nineteenth century introduction of this vector and of avian pox in Hawaii followed by a later introduction of avian malaria is thought to be the main reason for the dramatic decline of Hawaiian endemic birds throughout the twentieth century (Warner 1968; van Riper et al. 1986, 2002).

The presence of *C. quinquefasciatus* in the Galapagos Islands is considered to be a serious threat to its endemic fauna because of the role of this mosquito in wildlife disease transmission elsewhere (Whiteman et al. 2005; Causton et al. 2006). Multiple parasites vectored by this mosquito are already present in Galapagos, most notably avian pox viruses, *Plasmodium* parasites, and the nematode *Dirofilaria immitis* (see Sect. 3.4.1). However, its exact role in the transmission of these parasites remains unclear. The capacity of the Galapagos *C. quinquefasciatus* to transmit parasites has only been demonstrated for West Nile virus (Eastwood et al. 2011). Additionally, it is worth noting that a pool of 30 *C. quinquefasciatus* heads tested positives to avian pox virus in a PCR assay (Bataille A, Cruz M, Cedeno V, Cunningham AA, Goodman SJ, unpublished data), supporting its potential role in the mechanical transmission of this virus (Thiel et al. 2005).

A worldwide genetic survey of *C. quinquefasciatus*, including samples from the Galapagos Islands, was conducted using microsatellite markers (Fonseca et al. 2006). The Galapagos samples were genetically very similar to specimens from mainland Ecuador, supporting the idea of a recent colonization of the archipelago from this country. However, the study included only a small number of samples from one island (Santa Cruz), which was insufficient to fully understand the history of its presence on the archipelago or the risks of current and future introductions.

During the 2006–2007 airplane monitoring program, eight live *C. quinquefasciatus* mosquitoes were collected in airplanes arriving in Baltra and San Cristobal airports, evidence of their on-going introduction to the archipelago (Bataille et al. 2009b). The same authors sampled *C. quinquefasciatus* specimens across the Galapagos Islands and in mainland Ecuador, and used microsatellite markers to further assess the genetic similarity between the mosquito populations in the archipelago and mainland Ecuador, and to determine the pathways and frequency of introduction of this mosquito from the mainland to the archipelago. They showed that the *C. quinquefasciatus* populations in Baltra and San Cristobal (the two islands hosting airports connected to mainland Ecuador) were genetically more similar to mainland mosquito populations than to populations from Santa Cruz, Isabela, or Floreana Islands (Bataille et al. 2009b). Such a pattern is most likely the result of frequent introductions of mosquitoes via airplane, and of their successful integration into already-established populations.

Culex quinquefasciatus could also arrive in the archipelago with cargo boats arriving to Santa Cruz, San Cristobal, and Baltra islands. However, Bataille et al. (2009b) did not observe a strong genetic similarity between *C. quinquefasciatus* populations of Santa Cruz Island and mainland Ecuador, suggesting that *C. quinquefasciatus* introduction by boat is much less important than by airplane. Although airplane disinfection has been implemented for commercial flights bound to Galapagos since 2007 following World Health Organization guidelines, the increase in flights to the archipelago associated with tourism development still represents a major risk of parasite introduction with infected disease vectors.

3.5 Conclusions and Future Directions

Our understanding of parasite and vector colonization in Galapagos is incomplete. However, there are several well-studied examples (e.g., mosquitoes, avian hemosporidians, avian pox), which emphasize that all routes of introduction including natural colonization, colonization with a vertebrate host (a colonizer or migrant/vagrant), and anthropogenic colonization have been documented. We know the most about colonization of a few organisms of conservation concern, such as the mosquito species known as disease vectors elsewhere in their distribution. We lack specific information on colonization for the majority of parasites identified in Galapagos (see Table 3.2) and therefore can only speculate on arrival mode and evolutionary history.

In order to properly study parasite and vector colonization, research must extend to continental sister taxa or, in cases of non-endemic species, research must include organisms sampled outside their Galapagos range. The best approaches for studying colonization include detailed phylogeographic and population genetic approaches.

When possible, researchers should sample the entire parasite community in and on Galapagos animals and their closest continental relatives. By sampling parasite assemblages, we can reconstruct more accurate hypotheses about parasite arrival and divergence within Galapagos. For example, by examining all species of lice and mites found on the Galapagos flycatcher and their most closely related continental sister taxa, the Brown-crested flycatcher, Sari et al. (2013) concluded that the suite of ectoparasites probably arrived with the ancestor of the Galapagos flycatcher and that only one mite species had diverged in morphology since arrival to Galapagos. Sampling only the divergent mite could have led to a different conclusion. Furthermore, vertically transmitted and closely host-associated parasites can be used as additional evidence for revealing host evolutionary history (Whiteman and Parker 2005). Thus, studying parasite colonization adds more information about the evolutionary history of Galapagos than simply an answer to how that particular parasite colonized the islands.

When inferring whether a parasite arrived by natural colonization or by human introduction, it is important to predict which ones may represent a greater threat to the Galapagos native fauna. Endemic fauna have been isolated in the archipelago for a long time, and may have lost their ability to mount immune responses against recently introduced parasites. So knowledge about arrival and transmission of introduced parasites is essential and urgent for proposing conservation strategies and the prevention management in Galapagos.

Continued—and perhaps expanded—monitoring programs are needed to prevent further human-aided parasite introduction. Generalist parasites with robust free-living stages or free-living vectors are of greatest concern, as they could be brought in on boats or in cargo holds of planes. Host-specific parasites are of less concern because their most plausible route of introduction is with the host, and even if they arrived, they are less likely to establish on a novel host. There is still concern about the introduction of parasites via migratory birds, but there is little that can be done to prevent parasite spread from migratory sources, except regular avian screening (see Fig. 3.7). For example, there is concern about the potential arrival of *Plasmodium relictum*, the pathogenic hemosporidian species that has contributed to the decline and extinction of many Hawaiian honeycreepers. *Plasmodium relictum* could arrive to Galapagos via an infected bird, but in order for the parasite to establish, a competent vector is needed. Unfortunately, the vector of this lineage in Hawaii, *Culex quinquefasciatus*, is well established in Galapagos. Preventing the colonization of *P. relictum* would require eliminating the introduced *C. quinquefasciatus*, which is not a simple task. Both *C. quinquefasciatus* and native *Aedes taeniorhynchus* mosquitoes are competent vectors for West Nile Virus, which has not yet colonized the archipelago.

Collaboration should be a top priority as more research is conducted on parasites in Galapagos. Research teams working in Galapagos do not always interact or coordinate during their research expeditions. There are many local and international groups collecting samples in the islands and many of these samples could be used for multiple purposes, beyond the original reason for the collection. For example, blood collected for a population genetic study could be screened for hemosporidian

Fig. 3.7 Screening domestic and migrating ducks for diseases threats to Galapagos fauna such as avian influenza (Photos: Arnaud Bataille)

parasites. Because it is expensive and time-intensive to sample many islands within the Galapagos, coordination of research among different teams can improve sampling effort. Increased communication, better database compilation and sharing, and more comprehensive sampling could vastly improve our knowledge about the parasites in the Galapagos archipelago and how they got there.

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